Early Paleozoic colonisation of the land: evidence from the Tumblagooda Sandstone, Southern Carnarvon Basin, Western Australia

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The early Paleozoic Tumblagooda Sandstone outcrops principally in the vicinity of the Murchison River in Kalbarri National Park, Western Australia. It contains a great variety of trace fossils that provide a unique insight into the activities of early invaders of the terrestrial environment, and may record one of the earliest known freshwater and terrestrial ecosystems. The traces reveal that this nascent terrestrial fauna was dominated by arthropods. In outcrop the sandstones are more than 1 km thick and comprise predominantly mixed fluvial and eolian deposits. The age of the Tumblagooda Sandstone has been the subject of much debate. Initial analysis of the trace-fossil assemblage suggested a Late Silurian age. Preliminary work on conodont faunas in sediments of the conformably overlying Dirk Hartog Group also indicated a Silurian age. However, arguments have been made for an older, Ordovician age based on paleomagnetic and pedostratigraphic studies. In this review it is argued that deposition is linked to the known ages of regional uplift of the hinterland, and thus inferred to be Early to mid-Silurian. A previous study recognised two distinct trace-fossil assemblages. One, comprising a mixture of burrows and arthropod trackways, represents a freshwater/terrestrial ecosystem that inhabited sands interpreted as having been deposited in broad, low sinuosity, braided fluvial channels, between mixed eolian and water-lain sandsheets, small eolian dunes and flooded interdune, and deflation hollows. The major bioturbator was *Heimdallia*. Other burrows include *Tumblagoodichnus*, *Beaconites* and *Diplocraterion*. A variety of arthropod trackways, predominantly *Diplichnites*, formed on water-lain sands and foreset beds of eolian dunes. Other tracks include *Siskemia* and possible examples of *Paleohelcura* and *Protichnites*. Other arthropod traces include *Rusophycus* and *Cruziana*. Likely arthropod track makers include myriapods, eurypterids, euthycarcinoids and xiphosurids. A single trackway is interpreted as having been made by a tetrapod and as such pushes back the record of this group from the mid-Devonian to the Early–mid-Silurian. This trace fossil assemblage can be assigned to the *Scoyenia* ichnofacies. A second trace fossil assemblage, assignable to the *Skolithos* ichnofacies occurs higher in the section, in strata traditionally interpreted as having been deposited in a marginal fluvial-marine environment. The ichnofacies is dominated by burrows, especially *Skolithos*, but also *Diplocraterion*, *Daedalus* and *Lunatubichnus*. Rare locomotory traces are assignable to *Diplichnites* and *Aulichnites*. Preservation of the arthropod trackways in the *Scoyenia* ichnofacies was facilitated by the nature of the fluvial/eolian environment. Many of the tracks show indication of having been created subaerially on wet sand surfaces, and preserved by a covering of fine, eolian sand. The presence of extensive dwelling burrows and terrestrial trackways in the *Scoyenia* ichnofacies represents arguably the earliest known freshwater/terrestrial ecosystem. Moreover, it supports the view that one of the major steps in evolution, the colonisation of land by animals, may have been from rivers, rather than directly from the sea.

KEYWORDS: arthropods, Paleozoic, terrestrialisation, tetrapods, trace fossils.

INTRODUCTION

Covering an area of more than 7000 km² on the western margin of the Precambrian Yilgarn Craton, the early Paleozoic Tumblagooda Sandstone straddles both the Southern Carnarvon and Perth Basins. Although its actual age is the subject of much debate (see below), this thick sequence of sandstones remains the earliest known Phanerozoic deposits preserved in these marginal sedimentary basins. Iasky *et al.* (1998) pointed out that seismic data indicate that the Tumblagooda Sandstone is about 3500 m thick in the southern part of the Gascoyne Platform, a sub-basin in the Southern Carnarvon Basin. The unit thins significantly to the north, away from the sediment source. The Southern Carnarvon Basin itself was an interior-fracture basin that opened to the north and formed as a consequence of rifting along the western

margin of the Yilgarn Craton (Hocking & Mory 2006). As such, the Tumblagooda Sandstone records the first sedimentological evidence for the initiation of this rifting along the western Australia margin during the early Paleozoic.

The Tumblagooda Sandstone is dominated by iron oxide-rich quartz arenites that have variously been interpreted as having been deposited largely in a terrestrial setting, predominantly braided fluvial and eolian, with minor marginal marine input (Trewin 1993a, b) or in a mixed fluvial and tidal marine environment (Hocking 1991; 2000; Hocking *et al.* 1987). These different interpretations are discussed further below. These sediments were deposited over a very wide area that extended from at least 150 km south of Kalbarri into the northern part of the Perth Basin (Hocking & Mory 2006) to more than 700 km north, near Onslow (Evans *et al.* 2007). Although the upper and lower boundaries of the Tumblagooda Sandstone are not exposed in outcrop in

the Kalbarri region, in the subsurface the sandstones are known to be conformably overlain by shallow-water limestones and dolomites of the Silurian Dirk Hartog Group (Mory *et al.* 1998). The formation is seen to rest unconformably on Precambrian basement west of the Northampton Complex (Hocking 1991 p. 6, figure 4).

On the basis of the excellent exposures of the Tumblagooda Sandstone for some 70 km in the gorge of the Murchison River in Kalbarri National Park, and in the coastal gorges to the south of Kalbarri (Figure 1), Hocking (1991) subdivided the 1300 m of sedimentary rocks exposed in these areas into four discrete packages, which he termed Facies Associations 1 to 4. This subdivision has been accepted and utilised by all subsequent workers. While there is consensus that the earliest, Facies Association (FA)1 and third, FA3, represent braided fluvial deposition, there is debate on the environment of deposition of FA2, a more variable unit that is dominated by thin-bedded sandstones. The youngest package, FA4, is generally accepted to represent a marginal marine environment of deposition.

Some parts of the Tumblagooda Sandstone, typically FA2 and FA4, contain rich trace-fossil assemblages, with a high diversity of trackways and burrows in both facies associations, with tracks especially dominant in FA2 and burrows in FA4 (Trewin & McNamara 1995). There is ample evidence from the style of preservation of some of the trackways that these were made by animals, predominantly arthropods, out of water. As such, these early Paleozoic redbed sandstones contain some of the best evidence anywhere for the early colonisation of land by animals, while the presence of a variety of established dwelling burrows in FA2 may record the earliest evidence for the establishment of a freshwater ecosystem.

In addition to discussion on the interpretation of the

environments of deposition of the sandstones, there has been much debate concerning the age of the unit, with suggested ages ranging from Cambrian to Devonian. Given its importance in our understanding of the earliest terrestrial ecosystems, defining the age of these sediments is of paramount importance. In this review an alternative methodology is proposed for establishing the age of the Tumblagooda Sandstone. The only papers to date on the fauna of the Tumblagooda Sandstone are descriptions of the trace-fossil fauna by Öpik (1959) and Trewin & McNamara (1995), and description of the lone body fossil found in this unit (McNamara & Trewin 1993). In this paper I review the trace-fossil fauna, drawing particularly on the work of Trewin & McNamara (1995), and discuss the implications of the fauna in the context of it being one of the earliest freshwater ecosystems.

AGE OF THE TUMBLAGOODA SANDSTONE

Any attempts to establish a definitive age for the Tumblagooda Sandstone are constrained by the present inability to obtain radiometric dates other than from detrital zircons, and the lack of any body fossils that would enable a refined biostratigraphic age. The only body fossil found to date, a single specimen of the euthycarcinoid *Kalbarria brimmellae* (McNamara & Trewin 1993), provides no help in this regard (Figure 2). Neither does the extensive trace-fossil assemblage in the sandstones (Trewin & McNamara 1995), with the ichnofacies being representative only of particular early Paleozoic ecosystems and not being age-diagnostic. Attempts have been made to infer the age from reliable biostratigraphic data from overlying lithostratigraphic
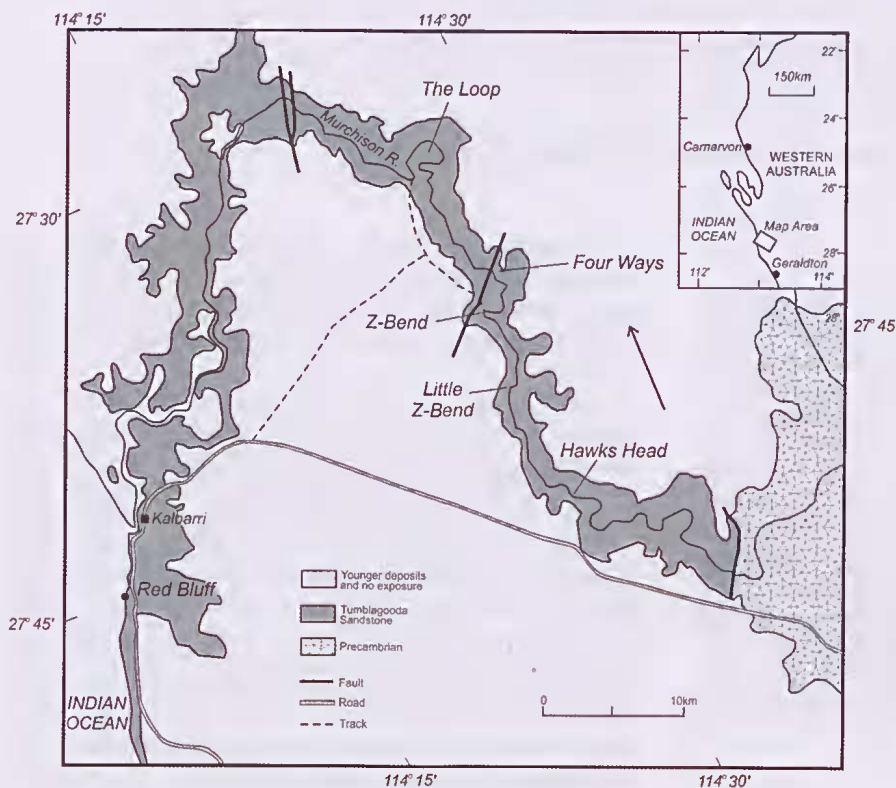

Figure 1 Map showing principal outcrops of the Tumblagooda Sandstone around the Murchison River (based on Trewin 1993a figure 1).

Figure 2 The euthycarcinoid *Kalbarria brimmellae* McNamara & Trewin 1993 from the Tumblagooda Sandstone. Holotype and only known specimen, WAM 90.158 from top of gorge at the eastern end of The Loop; FA2. Photo by K Brimmell.

units (Mory *et al.* 1998). However, even using this technique there are age discrepancies and they only provide a minimum age estimate.

The formations in the Dirk Hartog Group, which conformably overlies the Tumblagooda Sandstone in boreholes to the north of the main outcrops in the Murchison River area, have yielded conodont faunas. Philip (1969) interpreted these as indicating a Late Silurian (mid to late Ludlow) age, which implies the Tumblagooda Sandstone is earlier Silurian at the youngest. A minimum Silurian age is also suggested by conodonts that were obtained from the Dirk Hartog Group from mineral boreholes and stratigraphic wells. Six specimens from the Wandagee 1 well, located about 400 km north of Kalbarri, and first identified as *Teridontus nakamurai* by Gorter *et al.* (1994), were regarded as an undescribed species of *Teridontus* by Mory *et al.* (1998). As Mory *et al.* pointed out, this genus has a range of Late Cambrian to Early Ordovician and thus could be reworked, as all conodonts from elsewhere in the Dirk Hartog Group are Early Silurian or younger. They caution against using these elements as age-diagnostic indicators. More reliable material was derived from the Dirk Hartog Group in other wells (Mory *et al.* 1998). The oldest of this material includes *Ozarkodina broenlundi*, a species that occurs within the

Pterospathognathus celloni zone, which is mid-Telychian (late Llandovery) in age (about 431 Ma: Ogg *et al.* 2008). The Tumblagooda Sandstone would thus be older.

A maximum age constraint is provided by a Pb mineralisation age of 434±16 Ma (Llandovery) obtained in the adjacent Northampton Inlier (Richards *et al.* 1985). There is no evidence of Pb mineralisation in the sandstones (Hocking 1991), indicating that mineralising fluids passed through the metamorphic rocks of the Northampton Inlier prior to the deposition of the Tumblagooda Sandstone. Byrne & Harris (1993) also observed that any models invoking post-Tumblagooda Sandstone mineralisation are not supportable by the evidence. However, Retallack (2009) stated that what he interpreted as gossans in the Tumblagooda Sandstone points to the influence of the mineralisation on the sandstones and a much older age for the formation. These were considered by Hocking (1991) to be simply relatively young ferruginous cementation of conglomeratic breccias by fluids leaking along fault planes, after gorge incision. No anomalous Pb values are known.

Despite this seeming relatively strong support for an Early Silurian age for the limestones that overlie the Tumblagooda Sandstone and a Silurian age because of the lack of mineralisation, other workers have suggested that there is further evidence for an older, pre-Silurian, age for the sandstone. Paleomagnetic studies of the Tumblagooda Sandstone favour an Ordovician age of deposition. A paleomagnetic reverse-to-normal transition was identified by Schmidt & Hamilton (1990) in the conglomeratic Gabba Gabba Member from FA4 in coastal outcrops south of Kalbarri and was correlated with the basal Silurian (444 Ma: Ogg *et al.* 2008), suggestive of a Late Ordovician age for the formation. Schmidt & Embleton (1990) further interpreted the position of the paleomagnetic pole at the time of deposition of the sediments. They argued that the paleomagnetic data do not support a Silurian pole position. They suggested, on the contrary, that the Tumblagooda Sandstone may therefore be anything from Cambrian to Ordovician in age. A recent outcrop gamma ray study of the Tumblagooda Sandstone assumed a Late Ordovician age (Evans *et al.* 2007).

More recently, Retallack (2009) claimed that paleosols are present in the Tumblagooda Sandstone, despite such features never having been seen previously by other workers. Both Hocking (1991) and Trewin (1993a, b), for instance, after undertaking exhaustive studies of the sedimentology of these sandstones, saw no evidence of soil-forming processes or paleosols. However, Retallack, working on the premise that depth of formation of nodular calcretes, which he claims he identified, is indicative of extent of levels of precipitation, interpreted 'pedostratigraphic spikes' in the Paleozoic across Australia. On the basis of this Retallack interpreted the Tumblagooda Sandstone as having been deposited over the entire Ordovician Period, a period of some 45 million years. Given the style of predominantly fluvial sedimentation in an environment when there was very little land vegetation cover (see below), it is extremely difficult to to see how this would have taken such an inordinately long period of time to be deposited.

None of these lines of evidence for the age of the Tumblagooda Sandstone are particularly rigorous. All

but the Pb mineralisation age of Richards *et al.* (1985) are compatible with or suggestive of a pre-Llandovery age, in other words it could be Early Silurian or Ordovician, or even earlier. An alternative strategy to establish the age of deposition of the Tumblagooda Sandstone is to look at the genesis of the sediments and ascertain whether the factors responsible for their accumulation can provide insights into their age of deposition.

A key feature of the Tumblagooda Sandstone is that it is the first known Phanerozoic deposition recorded in the Perth and Southern Carnarvon Basins, both of which lie to the west of the Precambrian Yilgarn Craton. As discussed below, the sandstones are a mixed sequence of predominantly sheet-braided fluvial sands (Hocking 1981, 2000; Trewin 1993a, b; Hocking & Mory 2006), and sandsheets, deposited either in a marine, tidal environment (Hocking 1979, 1981) or as eolian sandsheets and dunes (Trewin 1993a, b). Such a 'sheet-braided' style of siliciclastic sedimentation is characteristic of many early Paleozoic river systems due to the absence of an effective land vegetation up to this time (Cotter 1978; Hocking 1991; Davies & Gibling 2010).

Paleocurrent data from fluvial episodes in the Tumblagooda Sandstone indicate a general northwesterly trend of sediment transport (Hocking 1991; Trewin 1993a, b). Therefore onset of the fluvial sedimentation that characterises the Tumblagooda Sandstone must have been brought about by initiation of regional uplift to the southeast of its area of deposition (Hocking 1991 p. 22). Indication of a source of the sediments from the south also comes from an analysis of reworked zircons in the sandstones. These all suggest derivation not from nearby parts of the Yilgarn Craton to the east (Cawood & Nemchin 2000), but from the south, probably from the uplifted Prydz–Leeuwin Belt, from which the regional paleoslope produced a northward-flowing drainage system (Veevers *et al.* 2005). As noted by Iasky *et al.* (1998), the sediments are correspondingly much thicker in the south.

Evidence for the timing of uplift of these southern terrains that provided the sediment comes from the ages of reheating of the biotites. Libby & De Laeter (1998) showed that erosional rebound following collision of the Australo-Antarctic and Indian–Antarctic domains resulted in biotite Rb/Sr dates being reset at about 430 Ma when the western margin of the Yilgarn Craton and the Albany Mobile Belt moved through the 320° isotherm. Further support for a period of uplift during the mid-Silurian comes from Nemchin & Pigeon (1999) who used U–Pb systems of apatites from granites from the western part of the Darling Range Batholith to show that there was a disturbance at about 420 Ma, suggestive of heating and uplift along the western margin of the craton.

These lines of evidence point to deposition of the Tumblagooda Sandstone during the Silurian, probably during the Llandovery. Of these, Pb mineralisation at 434±16 Ma in the nearby Northampton Inlier and not in the Tumblagooda Sandstone, provides a maximum age constraint. Secondly, conodonts in the overlying Dirk Hartog Limestone have a maximum age of late Llandovery (about 431 Ma). Lastly, there is the Rb/Sr biotite date of about 430 Ma resulting from heating associated with uplift that may have led to the production of the Tumblagooda Sandstone sediments.

TUMBLAGOODA SANDSTONE DEPOSITIONAL ENVIRONMENT

Major depositional cycles

Two significant sedimentary cycles have been recognised in the Tumblagooda Sandstone (Hocking 1991; Trewin 1993a, b). The first cycle consists of thick fluvial deposits (FA1) overlain by finer, but still sand-dominated, deposits (FA2) interpreted as mixed wholly freshwater, eolian and fluvial facies (FA2) (Figure 3) (Trewin 1993a, b; Trewin & McNamara 1995) or as marginal marine, tidally dominated facies (Hocking 1991, 2000). The sediments of FA1 are predominantly trough cross-bedded medium- to coarse-grained sandstones. As indicated, paleocurrent data
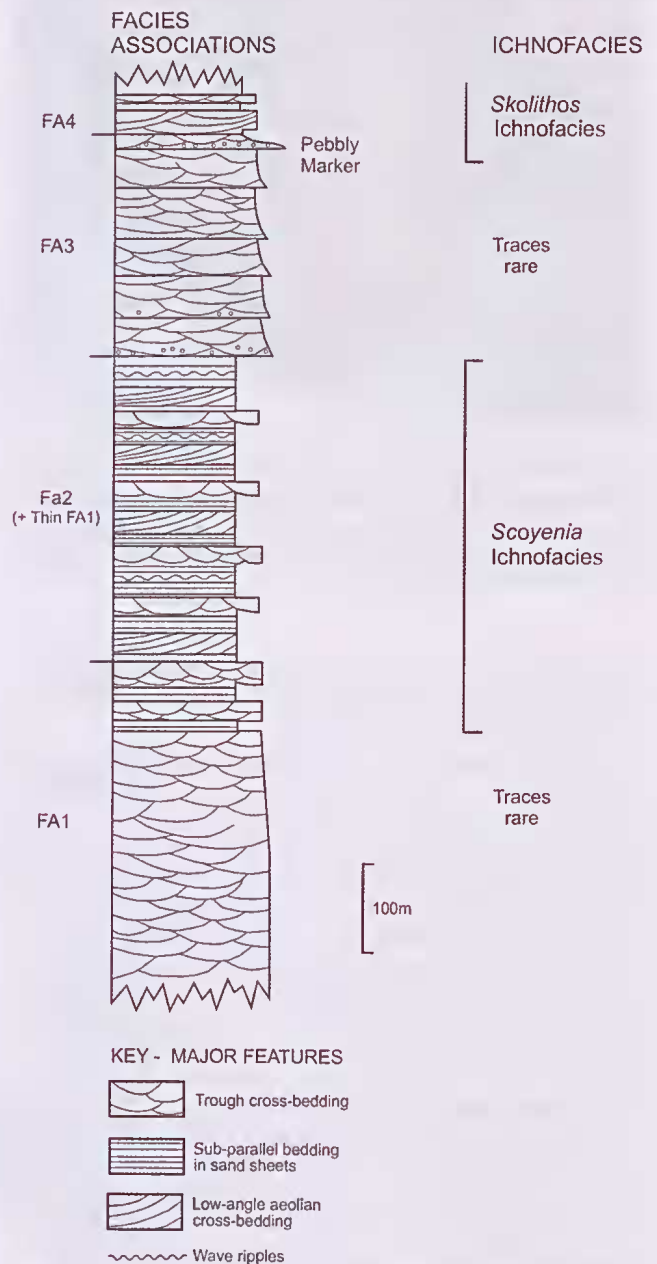

Figure 3 Composite diagrammatic section showing lithofacies and corresponding ichnofacies in the Tumblagooda Sandstone (based on Trewin 1993a figure 2, utilising data from Hocking 1979, 1981).

suggest a northwestward direction of transport, the sands having been deposited in large sheet-braided lobes (Hocking 1991, 2000). Sediments of FA2 consist of mainly fine- to medium-grained thin-bedded sandstones, and are much more variable in their style of deposition. The difference in interpretation of the depositional setting of FA2 is important in understanding the significance of the trace-fossil fauna in models of early colonisation of the continental environment during the early Paleozoic. Arguments in support of the first interpretation are presented below.

Trewin (1993a, b) and Trewin & McNamara (1995) considered that the transition from FA1 to FA2 represented an overall reduction in fluvial processes and an increase in eolian processes in the younger sediments. Such a change in depositional style could reflect a reduction in rainfall resulting in increasing aridity and thus a reduction in sediment supply (Trewin 1993a). Trewin further suggested an alternative scenario, a shift in the area of fluvial deposition.

The second cycle of FA3 to FA4 is marked by the sudden reappearance of coarser, fluvial sandstones, suggesting a rejuvenation of the source area (Hocking 1991). Lithologically the sediments are very similar to those deposited in FA1, though FA3 differs from FA1 in having clear metre-scale fining-upward cyclicity. The transition from FA2 to FA3 could have arisen from an increase in paleoslope, resulting in an increase in depositional energy and thus grainsize (Trewin 1993a). Alternatively it may reflect increases in rainfall in the source area of the sediments to the southeast. Hocking (1991) considered that depositional energy levels were higher for the deposition of FA3, compared with FA1.

Sediments of FA3 are replaced higher in the section by sediments of FA4. These are a series of fining-upward cycles 0.5–2 m thick, from medium-grained sandstones to much finer siltstones. FA4 probably represents a higher energy fluvial–marine transition, although further research is required to validate this hypothesis.

Sediments of FA2

EOLIAN SANDSHEETS AND DUNES

FA2 is composed primarily of subparallel, bedded sandsheets up to 2 m thick, with internal laminae 1–5 cm thick, with low-angle cross-bedding typical of deposition in an eolian setting. The sandsheets are bounded on their upper surfaces by low-angle truncation surfaces and have inverse-graded millimetre-scale laminae characteristic of eolian ripples (Trewin 1993a). Bedding planes show adhesion ripples and eolian deflation ridges. Beds lacking the fine lamination often show wave ripples, typical of structures formed in shallow water. Many display evidence of subsequent exposure.

The low-angle (generally <20°) cross-bedding occurs in beds up to 2 m thick of well-sorted, fine- to medium-grained sandstones. The bases of the cross-bedded units grade into sandsheets which commonly show wind-ripple lamination (Trewin 1993a). From analysing patterns of cross-bedding Trewin (1993a) was able to demonstrate the straight-crested architecture of the dunes, many of which were at least 100 m wide. The upper surfaces of cross-bedded units locally show corrugations produced by

eolian scour. Moreover, foresets may be covered by low-amplitude eolian ripples. As Trewin (1993a) has pointed out, slip-face orientations of the cross-bedding consistently are directed to the southeast, rather than the northwesterly trends seen in the fluvial trough cross-bedding. This supports the notion that these were eolian dunes facing obliquely up the paleoslope. Between the dunes active deflation is thought to have occurred, resulting in the subsequent development of interdune pools. The absence of current ripples in these bodies of water led Trewin (1993a, b) to argue that flooding was not due to fluvial activity, but was generated by a more passive rising water-table following drier phases of eolian sand movement. Some shallow interdune pools show evidence of microbial mat development.

Much of the argument for the early establishment of a terrestrial freshwater ecosystem hinges on trace-fossil evidence from FA2. The rich trace-fossil assemblage in FA2 is characterised by an extensive suite of arthropod trackways (see below). The manner of their preservation lends support for the view that there was extensive eolian activity during the deposition of this facies. The trackways occur mainly in the sandsheet facies, as well as on sloping surfaces of small dune features. They are often on flat-topped rippled surfaces. Preservation of the trackways is very variable, from poorly defined clusters of footfalls that have merged into a single depression, to very commonly exquisitely preserved detail of each individual footfall, with small, discrete mounds of sediment piled up behind the imprint (Figure 4), or in the case of what is interpreted as a set of vertebrate footprints, finely preserved sand splashes produced by a more rapid flicking of the sediment during the locomotion stroke (see below).

The walls of the footprints are often steep-sided to vertical, the sand being sufficiently cohesive to the moment the foot was withdrawn from the sediment to retain the exact shape made by the footfall. Such preservation can only occur with such frequency on wet sand surfaces that are subaerially exposed (Hocking 1991 p. 33). Surface tension between sand grains will provide a rigid cohesive force over a wide range of degrees of water saturation (Scheel et al. 2008). Only in the extremely wet or extremely dry sands will the footprints be ill-defined. This wide range in water saturation levels that result in binding of sediment grains by surface tension is part of the reason for the preservation of so many trackways throughout FA2.

The other reason is that exposure by natural weathering of the tracks occurs at boundaries between abruptly changing grainsizes, almost invariably the footprint-imprinted sands being overlain by appreciably finer, very well-sorted sands. Such sands are here interpreted as having been deposited by eolian agencies. The deposition of the very fine sand is likely to have occurred as the wind velocity decreased, passively covering and protecting the finest details of the footprints. Hocking's (1991) scenario of deposition in a tidal flat is not supported by the style of footprint preservation. Any trackways made on an exposed tidal sand flat are likely to have been destroyed by the incoming tide. Although it could be argued that mud drapes during periods of still water could conceivably preserve such tracks, there is no sedimentological

Figure 4 *Diplichnites* trackway showing steep-sided footprints arranged in groups of three, with the inner pair getting out of phase with the outer pair because of their shorter length, causing them to have a greater stride distance. Note also the small mounds of sand pushed up by the appendages, confirming movement direction being from bottom to top. WAM 84.1634. From top of the gorge at The Loop; FA2. Scale bar 100 mm. Specimen on display in *Diamonds to Dinosaurs* Gallery, WA Museum, Perth. Photo by K Brimmell.

evidence in the Tumblagooda Sandstone for such events. Moreover, the lack of herring-bone cross-stratification in the sediments further argues against a tidal influence.

FLUVIAL SANDS

Interbedded with the sandsheets are moderately sorted medium- to coarse-grained sandstones, generally up to 3 m thick, but up to 8 m in some instances, with occasional mud clasts and small pebbles. These have been interpreted (Hocking 1991; Trewin 1993a, b) as having been deposited in fluvial channels and sheets. These units probably represent a sequence of flooding events, single events being represented by thinner cross-bedded units up to 50 cm thick. The thicker units are the equivalents of FA1 and locally show soft-sediment deformation (Hocking 1991). Trough cross-bedding is commonly seen in these thicker units, and erosional features occur at their bases. There is little evidence of the establishment of incised channels, deposition being mainly braided. Upper surfaces sometime show evidence of burrowing activity, suggesting periods of stability before the next flooding event.

Hocking (1981, 1991) traced thicker units for up to 3 km in a downcurrent direction. Architecture of the flows was sheet-like, diminishing in thickness downstream. In FA1 and FA3 current direction was generally northwesterly (Hocking 1991). In FA2 fluvial beds northwesterly paleocurrents are present in the coarser facies, but the interspersed sandsheets and dunes do not show the same northwesterly direction of flow. Rather, fluvial flow was to the southwest. Trewin (1993b) explained this difference as being due to water flow having been constrained by the orientation of the dunes (which ran southwest to northeast), resulting in flow parallel to the dunes and hence to the southwest. Why flow was not to the northeast is not clear.

The fluvial beds are likely to have been deposited on a large sandy outwash area by sheet runoff (Hocking 1991). The trough cross-bedded units demonstrate that despite being relatively thin, the beds had great lateral extent; channel features were rarely developed; current direction was strongly unimodal; and top bounding surfaces were planar. Trewin (1993a) argued that such features point to variable stream discharge in an environment lacking any resistant sediment-binding agent, such as plants, mud or early cement. Deposition at a time before any appreciable covering by land plants in the absence of vascular plants minimised channel stabilisation by plant roots (Davies & Gibling 2010). Deposition was almost entirely of medium- to coarse-grained sands, with little mud or silt being retained. This suggests that energy levels during stream flow were sufficiently high to transport finer grained sediments more distally into the marine environment.

Trewin (1993a p. 397) argued that it was likely that 'the water table exerted a strong influence on deposition of the aeolian sandsheet facies in that it would have provided a downward limit to deflation processes'. Due to the permeability of the Tumblagooda sands, the water-table is likely to have risen appreciably during periods of high discharge, resulting in deflation hollows and interdune areas flooding and producing short-lived pools of water in which some small arthropods were able to feed and flourish. Where they resided after the pools

dried out is not clear. Either they were sufficiently mobile to move to other pools, or were able to aestivate in the sand or perhaps, like some modern-day notostracan crustaceans, laid eggs which hatched out when the pools were reactivated.

TUMBLAGOODA SANDSTONE ECOSYSTEM: ICHNOFABRICS AND THEIR IMPLICATION FOR FRESHWATER DEPOSITION

In their description of the trace-fossil fauna of the Tumblagooda Sandstone, Trewin & McNamara (1995) identified 27 different types of trace fossils. The traces were assigned to two ichnofaunas: the *Heimdallia–Diplichnites* Ichnofauna, present in FA2, and the *Skolithos–Diplocraterion* Ichnofauna, present in FA3 and FA4 (Trewin & McNamara 1995 figure 6). Trace fossils are absent in FA1. The various trace fossils that have been described can be categorised based on the behaviour of the animals that made them. These are: (i) locomotory tracks thought to have all been made, with one exception, by arthropods; (ii) locomotory trails; (iii) resting traces; (iv) dwelling traces; (v) hunting (predation) traces; and (vi) feeding traces. This range of activities, particularly in the trace-fossil fauna present in the mixed fluvial–lacustrine–eolian FA2, provides support for the idea that this association of trace fossils comprises evidence of the establishment of a relatively complex freshwater terrestrial ecosystem in this part of the Tumblagooda Sandstone during the Early to mid-Silurian.

In this review I assign those traces that form the *Heimdallia–Diplichnites* Ichnofauna to the *Scoyenia* ichnofacies. This ichnofacies is confined to FA2. Buatois & Mángano (2004) pointed out how the ichnofacies model originally proposed by Seilacher (1963, 1967) (called by him 'facies' rather than 'ichnofacies'), can be applied to trace-fossil assemblages formed in both continental and marine environments. Seilacher (1967 p. 415) proposed a single ichnofacies for all continental environments, which he called the '*Scoyenia* facies' for 'non-marine sands and shales, often red beds, with a distinctive association of trace fossils'. This ichnofacies is characterised by the presence of arthropod trackways and bilobed traces and meniscate burrows. However, a number of authors have noted (Frey & Pemberton 1984, 1987) that this ichnofauna formed under rather distinct environmental conditions, typified by low-energy setting that oscillated between aquatic and non-aquatic, subaerial, conditions. Buatois & Mángano (2004) now recognise four continental ichnofacies, of which the *Scoyenia* ichnofacies is but one. It is redefined (Frey *et al.* 1984; Buatois & Mángano 1995, 2004) as consisting of horizontal meniscate backfilled traces produced by mobile deposit feeders; locomotion traces, both trackways and trails; vertical dwelling burrows; a mixture of invertebrate (predominantly arthropod), vertebrate and plant traces; low to moderate ichnodiversity; and localised high abundance.

The Tumblagooda Sandstone ichnofauna fulfills all of these criteria, apart from the absence of plant material, on account of the pre-vascular plant age of the formation. As Buatois & Mángano (2011 p. 75) have pointed out, the

abundance of meniscate traces and arthropod tracks is 'typical of sediments periodically exposed to air or periodically inundated, and intermediate between aquatic and terrestrial environments'. As I will discuss, the preservation of many of the trace fossils in the Tumblagooda Sandstone is due to their primary formation as traces in a subaerial environment, but at the margin of quiet bodies of freshwater.

Compared with the *Scoyenia* ichnofacies, the *Skolithos* ichnofacies in FA4 is far more restricted in its diversity. It is characterised by the dominance of vertical, cylindrical burrows made by suspension feeders or passive predators; occurrence of spreite U-shaped equilibrium burrows; abundant three-dimensional burrows with a major vertical component; scarcity of horizontal traces; low diversity; and variable abundance (Buatois & Mángano 2011). Although the *Skolithos*-dominated trace-fossil fauna of FA4 fits well in this diagnosis of the ichnofacies, it differs in one significant respect in that Buatois & Mángano (2011) have suggested that in fossil examples of the *Skolithos* ichnofacies horizontal traces are not preserved, due to the high energy of the depositional system. Although not described in Trewin & McNamara (1995), arthropod tracks have been found in the trace fossil assemblage in FA4, along with *Aulichnites* trails, as discussed below.

Scoyenia ichnofacies

ARTHROPOD LOCOMOTORY TRACES

The most diverse horizontal locomotory traces in the Tumblagooda Sandstone are those made by arthropods, consisting of essentially parallel rows of pits often many metres in length. Arrangement of pits made by multiple footfalls varies between rows of discrete sets of repeated groupings of imprints (allowing assessment to be made of the number of walking legs) to less well-defined sets where leg number of the originator cannot be ascertained due to overprinting of footfalls. These arthropod trackways vary greatly in size from a minimum observed width of 5 mm between rows of appendage imprints (Figure 5), to the largest at about 300 mm. There is appreciable variation in trackways in the number of

Figure 5 Smallest known example of *Diplichnites*. Field specimen in the bottom of the gorge, western side of The Loop; FA2. Diameter of coin 19.4 mm.

Figure 6 Large *Diplichnites* trackways, about 18 cm in width crossing rippled marked sand at The Fourways, Murchison River; FA2. The pair coming in from the left seem to coalesce and the resultant single track becomes deeper, losing definition, perhaps due to one arthropod having climbed on the back of the other. This scenario is supported by the tracks becoming shallower following separation of the tracks. It is a matter of pure speculation as to the nature of their behaviour. Ruler 40 cm long.
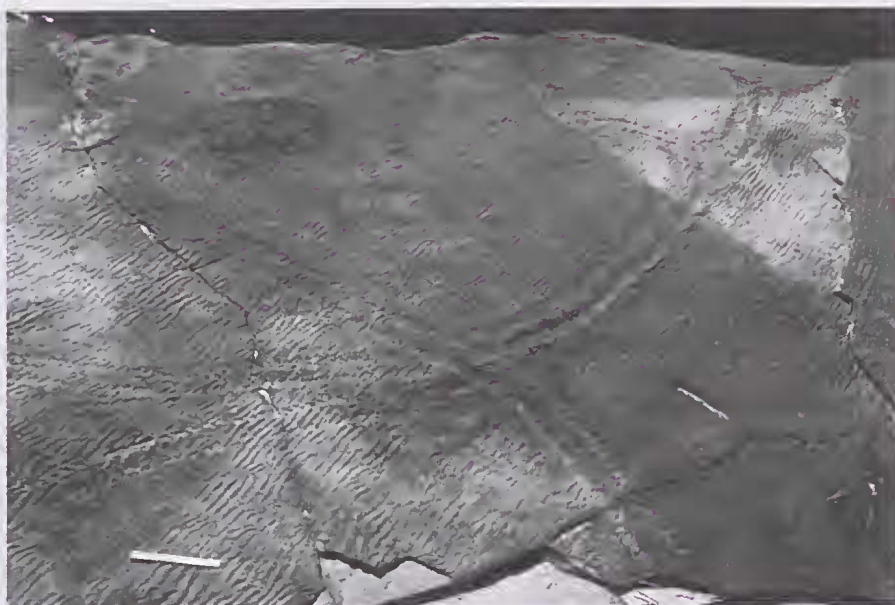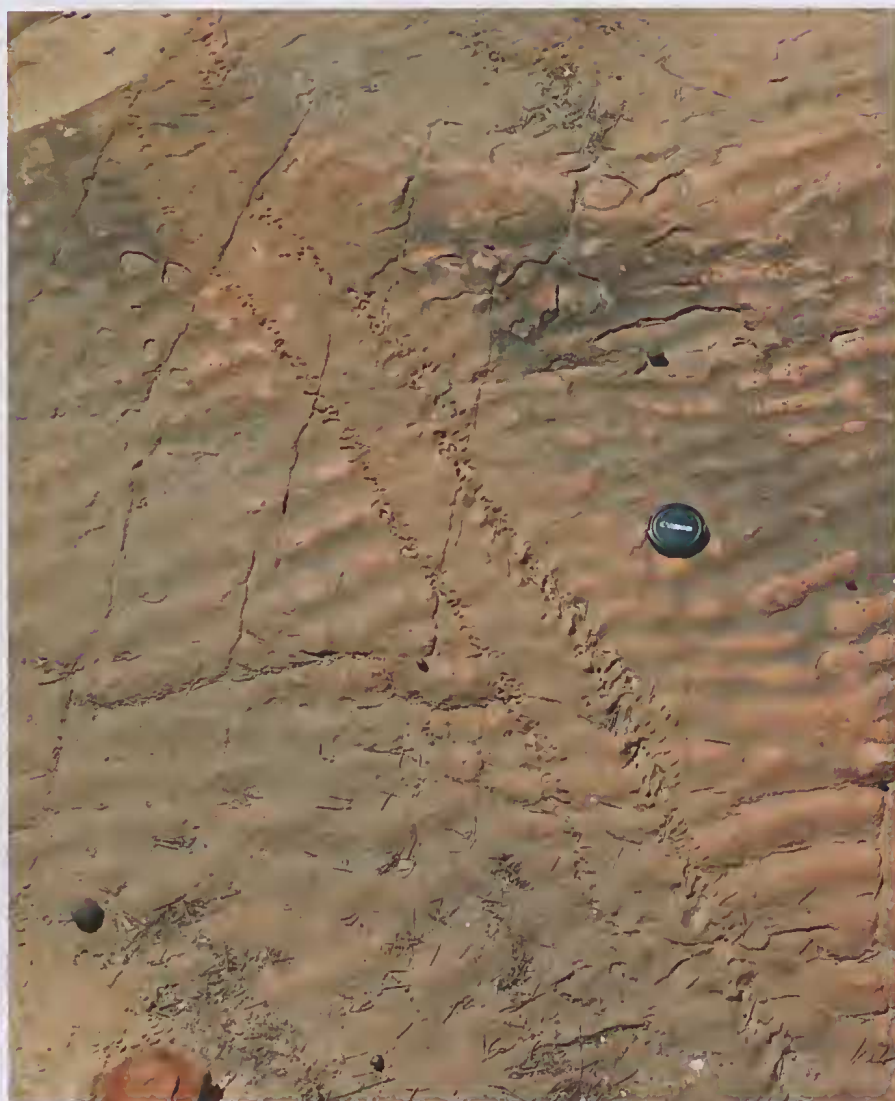

Figure 7 *Diplichnites* trackway crossing ripple marked surface showing repeated patterns of footfalls, suggesting formation by an arthropod, perhaps a euthycarinoid, with up to 11 pairs of legs. Field specimen at bottom of gorge on western side of The Loop; FA2. Lens cap diameter 55 mm.

imprints in each series, due to variations between taxa in the number of walking appendages; in spacing arising from variable speed of locomotion; and in degree of detail of the imprints, arising from differences in condition of the sediment at the time of formation of the imprints, in particular the degree of water saturation of the sediment. Those trackways made subaerially in sands that were either very dry or very wet are usually ill-defined, and series of imprints often merge together to form single, elongate grooves. However, trackways made in sands with a relatively wide degree of water saturation that provides sufficient surface tension to hold sand grains in contact, but not enough water to fill the pore space entirely, as this would cause collapse of the sand, can often show extremely good detail (Scheel *et al.* 2008). Thus not only can the numbers of appendages used in walking sometimes be calculated, but so too can the direction of stroke and the sequence of appendage usage.

Trackways can also show evidence of a single, broad central drag mark, or a pair of thin drag marks, produced by a ventral appendage or the tail. Forms without a central drag mark are the most common and are assigned to the ichnogenus *Diplichnites* (Figures 2, 4–10); those with a deep, single groove, and widely spaced groups of appendage imprints to ?*Paleohelcura* (Figure 11); those with a broad central drag mark to *Protichnites* (Figures 12, 13); while those with a pair of thin, parallel grooves were assigned to *Siskemia* (Figures 14, 15) by Trewin & McNamara (1995). Lengths of trackways vary from a few centimetres up to 10 m, the most spectacular being near Fourways where five well-defined tracks, each several metres in length, were formed on a wet, rippled surface (Figure 6).

A very wide variety of forms can be assigned to *Diplichnites*. In addition to morphological differences arising from a wide taxonomic diversity of arthropod track makers, this is also due to variability in behaviours of the track makers. This may, in part, be influenced by the consistency of the sediment across which they were walking and the consequent preservational effects in sands of variable water saturation levels. Trewin & McNamara (1995) somewhat arbitrarily subdivided the *Diplichnites* trackways into three groups, types A, B and C, based on track width and form of the imprints. These are likely to have been made by a variety of different arthropod taxa, morphological differences indicating perhaps by as many as 10 different types.

Diplichnites type A consists of small trackways, generally between 5 and 40 mm in width (Trewin & McNamara 1995 figure 19a). They are usually straight to gently curved, simple with a single row of evenly spaced conical to elongate imprints, which sometimes may be connected by a shallow groove. These tracks are in phase and the track rows are spaced at intervals a little less than half the external trackway width. Where the tracks curve they reveal a series of generally about five imprints at a very low angle to the midline. These tracks may have been made by a xiphosuran (Trewin & McNamara 1995).

Diplichnites type B trackways are the most common and are usually between 50 and 200 mm in width. They possess elongate imprints arranged at a high angle to the direction of travel. Often the imprints are superimposed. Two interpretations have been proposed as to how to

calculate the number of walking appendages possessed by the originator of the trackway. One suggests up to 11, the other interprets them as being in groups of three. Uncertainty arises from the fact that one of the group of three imprints gets out of phase with the other two (Figure 4). As a consequence, the out of phase imprints gets progressively closer to the midline before moving laterally as it gets back into phase with the other pair of imprints on a gentle sinusoidal curve. This could occur if this more anterior of the group of three appendages was appreciably shorter than the other two, which would be of similar length to each other.

In other types of trackways where oblique sets of up to 11 imprints occur, and where the two sets on either side of the trackway parallel one another, but are slightly offset to the main direction of the trackway (Figure 7), the originator of such tracks probably possessed up to 11 pairs of walking appendages (Figure 8). Given that the only body fossil found in the Tumblagooda Sandstone, *Kalbarria*, is a euthycarcinoid with 11 pairs of walking legs (Figure 2), it is not unreasonable to suggest that it could have been responsible for making many of these trackways. In those examples where sets of slightly

Figure 8 *Diplichnites* trackway showing repeated patterns of footfalls, suggesting formation by an arthropod, perhaps a euthycarinoid, with up to 11 pairs of legs. From top of the gorge eastern side of The Loop; FA2. Specimen on display in *Diamonds to Dinosaurs* Gallery, WA Museum, Perth. Scale bar 100 mm.

oblique groupings of 10–11 imprints are not parallel to each other and are both directed toward the midline, this is probably due to the offsets caused by the smaller appendage length of the anterior pair, the originator having just three pairs of walking appendages. As discussed below, there is evidence in some trackways of the originator having possessed at least one paddle-like pair of appendages. This, combined with locomotion on three pairs of appendages, suggests creation by a eurypterid.

Diplichnites type C trackways are the largest, generally between 200 and 300 mm in width (Figure 9). They are characterised by the possession of elongate, slit-like imprints directed at about 45° to the midline. The individual imprints may be up to 40 mm long and 15 mm wide. Two to three imprints occur in each group, but again they may get out of phase. As with other examples of *Diplichnites*, the imprints are in phase.

While the *Diplichnites* forms A–C generally have either imprints formed as conical pits, or as elongate slits, depending on the speed of locomotion of the originator, some forms attributable to *Diplichnites* have more complex imprints. Conical pits and slits would have been made by narrow arthropod walking legs that probably terminated in a relatively sharp point. However, trackways such as WAM 84.1647 have impressions made by much broader, paddle-shaped appendages. Specimen

Figure 10 Unusual *Diplichnites* trackway formed by an arthropod sinking into the sediment producing a drag mark made by the right hand side of its body. Limbs on the left side were probably held out almost horizontally as the animal tried to get purchase. On the right side imprints of paddles and semicircular grooves made by paddles suggest that the track might have been made by a eurypterid. WAM 84.1647 from near The Loop; FA2. Scale bar 30 mm.

WAM 84.1647 was made by an animal that may have been walking along the edge of sloping surface, causing the right hand side of its body to drag on the sand. Impression of the paddle-spaced appendage and of the sweeps it made as it propelled itself through the sediment are preserved (Figure 10). These are very reminiscent of eurypterid paddles (appendage VI).

Much less common than *Diplichnites* are arthropod trackways that also have a central drag mark, made either by a distal posterior terminal piece, or by a ventral sagittal appendage, such as a genital appendage (Braddy & Dunlop 1997). Although uncommon, such trackways show high diversity, varying in imprint architecture, and form and nature of the central drag mark. The largest is known from a series of overlapping trackways (WAM 84.1657) that were assigned to ?*Paleohelcura antarcticum* by Trewin & McNamara (1995). The trackways are rather disordered and, on the basis of the number of drag marks, represent four individuals (Figure 11). The most complete is about 160 mm in width, with individual footprints making large (up to 20 mm diameter) conical depressions that are up to 40 mm deep (Trewin & McNamara 1995). The central drag mark is up to 20 mm in width and in one instance shows a termination with a plug of sand at the end, suggesting that the structure that made the drag mark was able to be lifted from the surface of the sand during locomotion.

Figure 9 Large *Diplichnites* trackway about 25 cm in width. Field specimen, bottom of the gorge, eastern side of The Loop; FA2. Diameter of coin 28.5 mm.

Figure 11 ?*Paleohelcura* trackways with well-developed median grooves. WAM 84.1657, from top of the gorge near The Loop; FA2. Scale bar 100 mm. Photo by K Brimmell.

Trewin & McNamara (1995) suggested that these tracks could have been made by a scorpionid. However, the lack of a genital appendage in Paleozoic forms, such as *Gigantoscorpio*, argues against this interpretation. The similarity to an arthropod trackway from the Silurian of Ringerike, Norway described by Hanken & Størmer (1975) attributed to the eurypterid *Mixopterus*, suggest that the Tumblagooda trackway may also have been made by a eurypterid.

A distinctive, but very different, trackway from both *Diplichnites* and ?*Paleohelcura* is a relatively uncommon form attributed to ?*Protichnites* by Trewin & McNamara (1995). Examples are known that are about 75 mm in width. They are characterised by a series of closely spaced footprints that lie close to the midline, down which runs a broad drag mark. Each set of footprints consists of a group of ill-defined multiple footfalls that landed in roughly the same space, causing poor definition. These square to rectangular imprints are both closely and regularly spaced, about 25 mm apart, as well as being closely aligned to the broad, smooth drag mark which is up to 20 mm in width and is flat, apart from a

narrow, raised rim formed from the sediment having been laterally displaced during locomotion (Figure 12). It is not clear what organism was responsible for making this type of trackway. Despite the arguments of Collette *et al.* (2012), it is very unlikely to have been made by a euthycarcinoid.

In describing a series of trackways from the Cambrian Elk Mound Group of Wisconsin, which they assigned to *Protichnites*, Collette *et al.* (2012) inferred that trackways described by Trewin & McNamara (1995) from the Tumblagooda Sandstone support the assertion that the Elk Mound trackways were made by euthycarcinoids. This is not so. While ?*Protichnites* from the Tumblagooda Sandstone and *Protichnites* from the Elk Mound Group appear to be congeneric, no evidence or argument was presented by Trewin & McNamara (1995) to suggest that trackways with a central groove were made by euthycarcinoids. This group of arthropods is represented in the Tumblagooda Sandstone by *Kalbarria brimmellae* (McNamara & Trewin 1993) (Figure 2). From the same horizon as the body fossil, there are abundant trackways, and all are *Diplichnites*. In other words they lack a central drag mark. Moreover, where it is possible to ascertain the number of repeated sets of appendage imprints, these show the possession by the track originator of 11 pairs of appendages. This is the number of legs possessed by *Kalbarria*.

Figure 12 ?*Protichnites* trackway showing closely spaced footfalls and broad median groove. Trackway crossing surface with *Heimdallia* burrows. WAM 97.952; FA2. Scale bar 50 mm.

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Figure 13 Unnamed trackway probably made by the arthropod responsible for the ?*Protichnites* trackways walking through poorly consolidated rippled sands. Field specimen, top of the gorge at The Loop, north of Nature's Window; FA2. Pen 12 cm long.

Figure 14 *Siskemia* trackway showing distinctive thin double grooves between footfalls. Field specimen near Z Bend; FA2. Diameter of coin 28.5 mm.

One field example is known of an unnamed trackway that represents the ?*Protichnites* animal walking through very wet, rippled sand. Due to the high water-saturation levels there is no detail of individual footfalls, merely a pair of grooves representing where the animal ploughed through the sloppy sediment. The central drag mark forms a similar depth to the lateral drag marks made by the appendages (Figure 13).

Another uncommon arthropod trackway with a drag mark between the imprints of the footfalls is *Siskemia*. This generally small trackway, reaches up to about 90 mm wide and is typified by the possession of a pair of very narrow grooves. These can be up to about 15 mm apart. Sometimes they run down the midline (Figure 16), but in some examples they drift from side to side (Figure 14) or are close to one set of imprints (Figure 15). This suggests that the structure that made the drag marks was not fixed rigidly to the ventral surface of the arthropod body, but was articulated, allowing for a certain degree of lateral movement. Interestingly, in their discussion of the morphology of the genital appendage of the eurypterid *Baltoeurypterus tetragonophthalmus*, Braddy & Dunlop (1997) described the sexual dimorphism in this structure, highlighting that the form that may be the male possesses an appendage which terminally ends in a pair of strongly acuminate structures. If such an appendage were dragged along a sediment surface it would produce a trail very reminiscent of the central drag mark in *Siskemia*.
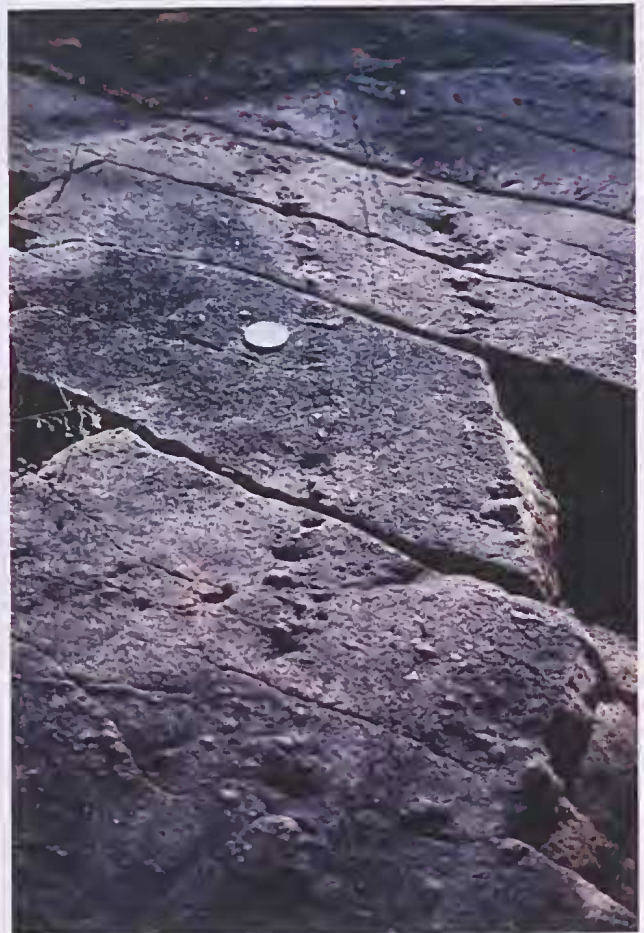
One example of *Siskemia* is known (Figure 15) that shows the faint double drag mark typical of the ichnogenus, and repeated patterns of nine footfalls. Moreover, this trackway was made by the arthropod walking along a strandline at the edge of a body of water. To one side are well-developed adhesion ripples, formed by the wind blowing over very wet sand, alongside a flatter, slightly drier sand surface upon which the *Siskemia* trackway was formed. Some *Diplichnites* trackways also show evidence of such a foraging strategy. A number of examples have been found where *Diplichnites* trackways similarly run parallel to paleostrand lines that flanked desiccating bodies of water. Such perambulations may reflect arthropods foraging along the margins of pools of water, and feeding upon stranded organic matter.

TETRAPOD LOCOMOTORY TRACE

One trackway (cast - WAM 12.12.1) in the FA2 facies is completely different from all other trackways ascribed to formation by arthropods. It is 18 cm wide and extends for 45 cm. Seven equally spaced imprints can be identified on its right side, and six on its the left. Individual foot impressions are rhombic in shape and very large, being 3.5–5 cm wide and 3 cm long, and set between 4 and 6 cm apart (Figure 16). The imprints are

Figure 15 *Siskemia* trackway with paired grooves closer to one set of footfalls. Individual walking along edge of body of water. To its left adhesion ripples formed by wind blowing over very wet sand surface. Field specimen from near The Loop; FA2. Scale bar 100 mm.

far larger than those made by individual arthropod footprints and completely different in shape. Even merged clusters of arthropod imprints which often develop when they have walked through very wet sand, are not as large as these and do not form the same shape. The rhomboidal form is unique among Tumblagooda Sandstone imprints. The fine details preserved in some of the impressions shows that they have not been formed by the coalescence of clusters of fine arthropod imprints. Opposite impressions are offset by about half an impression length. Four of the impressions show exquisite detail of what are interpreted as multi-digit imprints (Figure 17). The direction of limb movement during locomotion is shown by the orientation of the grooves left by the larger, adaxial digits, and by the orientation of the slightly sinuous, narrow ridges of sand that were formed as the sand was thrown sideways and backwards by the animal as it moved forward. The adaxial two digits were evidently the largest (both longer and broader than the others), and like the other digits they pointed anteriorly (Figure 17). The impressions made by these two larger digits are flanked by elongate grooves, seemingly made by four digit-like structures of similar size. These in turned are flanked by a pair of much smaller elongate impressions, indicating that the foot possessed a total of eight digit-like structures.

The 'sand splashes' created by the movement of the feet indicate that the trackway was made subaerially (Figures 16, 17). Such structures have never been observed in any arthropod trackways in the Tumblagooda Sandstone. Instead, arthropod footfalls only produced small mounds by the action of the fine, narrow appendages entering the sand at a high angle (Figure 4). Many of the impressions from specimen WAM 12.12.1 show evidence of multiple sand splashes from each propulsive event (Figure 17). Moreover, there is a direct correlation between each sand splash ridge

Figure 16 Plaster cast of mould of two sets of trackways (WAM 12.12.1). Running from left to right is a *Siskemia* track. Running across this is a trackway made by an animal with broad, digitate feet, interpreted as a tetrapod. Sand splashes present in bottom left corner of footprints on left hand side, and bottom right on right hand set of imprints attest to formation subaerially. These also show details of individual forwardly facing digits, which are broader closer to the midline. Based on field specimen downstream from The Loop; FA2. Scale bar 50 mm.

Figure 17 Close up of individual imprints on right hand side of trackway interpreted as having been made by a tetrapod. Photograph of field specimen, clearly showing imprints of digits and sand splashes caused by movement of the feet during locomotion. Field specimen downstream from The Loop; FA2. Scale bar 70 mm.

and the 'digit'. Whereas some sand splash ridge are straight, others are sinusoidal. This suggests independent movement of the digits.

Development of sand splash ridges implies reasonably rapid movement of the appendage during propulsion, with the wet sand being flicked out during the propulsive stroke. It is possible to suggest how the manus/pes rotated during propulsion from the orientation of the digit grooves and the corresponding sand splash ridges. The grooves extend almost exsagittally, but the sand splash ridges are orientated posterolaterally, indicating an initial posterior movement of the digits while in contact with the substrate, followed by a lateral rotation as the manus/pes was lifted from the substrate during the last part of its backstroke. The rotation of the manus/pes is responsible for the deeper excavation of the impression adaxially.

It is difficult not to come to the conclusion that the animal that made this track was tetrapodous and digitate. Such an interpretation clearly raises some major issues for our understanding of the sequence and timing of the origin of tetrapods and their activity on land. Currently the oldest described evidence for tetrapods are

trackways from the Middle Devonian of Poland (Niedźwiedzki *et al.* 2010). The imprints of the manus and pes of these trackways are very similar in appearance to the tetrapodous Tumblagooda trackway. Stride pattern is also comparable in the two forms. With the earliest skeletal evidence of tetrapods being the Late Devonian *Acanthostega* and *Ichthyostega* from east Greenland (Long & Gordon 2004), and the earliest undoubted terrestrial skeletal tetrapods not being know until the early Carboniferous, suggesting that terrestrial tetrapods existed in the early to mid-Silurian might seem foolhardy. But hopefully further material will be forthcoming from the Tumblagooda Sandstone to support the evidence provided by WAM 12.12.1, along with more empirical data concerning the age of the unit, to argue unequivocally that tetrapods were present in the Silurian and were part of the colonisation of land by animals. It could, of course, be argued that the tetrapodous condition in vertebrates may have originated more than once, the first time in Gondwana.

RESTING TRACES

In addition to locomotory behaviour, arthropod activity in the Tumblagooda Sandstone also includes evidence of scratch marks made by multilimbed arthropods, arising from either locomotion partially through the sediment, or from feeding activity. Resting traces that show evidence of the ventral elements of the arthropod are also relatively common. These often show an effective outline of the underside of the arthropod, particularly the scratch marks made by individual appendages (Figures 18, 19). There has been a tendency in the literature to ascribe the formation of *Cruziana* and *Rusophycus* to trilobites (Seilacher 1985; Buatois & Mángano 2011), but the presence of these trackways in a freshwater/eolian subaerial setting clearly shows that they can be made by other types of arthropods. One large *Cruziana* (WAM

Figure 18 Resting trace *Rusophycus*, possibly made by a euthycarcinoid. Pair probably made by same individual. Field specimen at bottom of the gorge, western side of The Loop; FA2. Lens cap diameter 55 mm.

Figure 19 Hunting trace *Selenichnites* (crescentic form on left) and resting trace *Rusophycus* (to its right), probably made by the same individual euthycarcinoid, possibly hunting for small organisms that occupy 1–2 mm diameter *Diplocraterion* burrows on same surface. Top of ridge, 500 km north of Nature's Window, The Loop; FA2. Pen 12 cm long.

dwelling traces and feeding burrows. The most common dwelling trace in the *Scoyenia* ichnofacies in FA 2 is *Diplocraterion*. Here it consists of very small U-shaped vertical burrows, with each burrow being only 1–2 mm in diameter (Figure 19), and set between 10 and 35 mm apart (Trewin & McNamara 1995 figure 22). The burrows are rarely more than 35 mm deep, and spreite are developed in the zone between the burrows (Schlirf 2011). *Diplocraterion* often occurs with *Rusophycus* and *Selenichnus* (see below) on the tops of fluvial channels.

Larger vertical burrows are represented by *Tigillites* (Trewin & McNamara 1995 figure 38), a much more irregular burrow system, with individual burrows about 10 mm in diameter, arranged in irregular rows up to 140 mm long. It has been suggested that these may represent failed attempts to establish more permanent feeding burrows by the organism that constructed *Heimdallia* (Trewin & McNamara 1995), as discussed below.

The largest burrows are horizontal to partially inclined meniscate burrows up to 150 mm wide and up to 500 mm in length that have been assigned to *Beaconites*. The burrows are straight to gently curved and infilled with backfilled packets of sediment (Figure 20). Morrissey & Braddy (2004) have suggested that *Beaconites* in the Lower Old Red Sandstone in south Wales could have been made by an eoarthropleurid myriapod. Fayers *et al.* (2010) have suggested that the enigmatic arthropod

92.635) has been found in the Tumblagooda Sandstone (Trewin & McNamara 1995). It shows a broad, double series of scratch marks angled at about 55° to the midline made by an arthropod with uniramous legs, as only one set of scratches is evident. Given the size (a width close to 80 mm), this was probably made by the same type of arthropod that made some of the larger *Diplichnites* trackways.

Examples of *Rusophycus* are more common. *Rusophycus trefolia* Trewin & McNamara 1995, was described from the Tumblagooda Sandstone on the basis of numerous relatively small, oval traces with paired scratch marks, or impressions of the appendages (Figure 18). These vary in width from 20 to 60 mm. Many are deeper at one end, which probably represents where the animal initially partially burrowed into the sand. Many show a trefoil shaped structure at one end, that may reflect the shape of the anterior feeding appendages (Figure 18). The scratch marks in these traces are more widely spaced than those that occur in *Rusophycus* made by trilobites, probably reflecting the uniramous nature of the originator, rather than the bilobed appendages of trilobites. The most likely candidate for the production of these small *Rusophycus* in the Tumblagooda Sandstone are euthycarcinoids, on account of comparable size and possession of multilimbed uniramous appendages.

DWELLING TRACES

Evidence that the environment in which the Tumblagooda Sandstone was deposited was, at times, conducive to the establishment of a permanent or semi-permanent freshwater ecosystem is shown not so much by the activity of arthropods walking across the surface of exposed sand flats, but by the establishment of

Figure 20 Dwelling burrow *Beaconites*. Field specimen at bottom of gorge, western side of The Loop; FA2. Lens cap diameter 55 mm.

Bennettarthra from the same Lower Devonian horizon could also have been responsible for the formation of the *Beaconites* and *Diplichnites* that occurs in association. It is probable that some of the organisms responsible for production of some of the smaller *Diplichnites* trackways in the Tumblagooda Sandstone were similarly responsible for the formation of the *Beaconites* burrows.

FEEDING TRACES

The most extensive vertical burrows have been assigned to *Heimdallia* (Figures 21–23). This is a complex burrow

Figure 21   Feeding trace *Heimdallia* showing well-developed spreite structures. WAM 84.1765a; FA2. Scale bar 50 mm.

form with both a vertical and horizontal component. It occurs in the sandsheet facies, sometimes in wave-rippled units or in microbial mats. In plan view the burrows are straight to extremely sinuous, with a width of 5–20 mm. The burrows are vertical to steeply inclined and generally about 120 mm deep, with backfill units about 5 mm thick. These reduce in inclination with depth (Trewin & McNamara 1995). *Heimdallia* can occur in large numbers, resulting in extensive bioturbation of beds many square metres in area. Individual beds are in the order of 120 mm thick, but these can occur in repeated units over 1 m thick (Trewin & McNamara 1995).

Bradshaw (1981), in describing similar *Heimdallia* burrows from the Devonian of Antarctica, considered that they were made by arthropods mining the sand, and extracting organic material. The extent of *Heimdallia*-rich beds in the Tumblagooda Sandstone implies that periodically the shallow-water bodies in which they formed were organically very rich, possible in algae or bacteria, or both. As Trewin & McNamara (1995) have suggested, this may explain why the sediment would have been sufficiently cohesive to preserve the burrows. In his study of Lower Carboniferous examples of *Heimdallia* from Ireland, Buckman (1996 p. 50) interpreted them as feeding structures 'formed from a horizontal basal tube by repeated cycles of probing and withdrawal in an upward vertical vector, with forwards movement occurring at the end of each cycle... resulting in the production of a 'spreite' structure.'

Another, much less common, burrow is *Didymaulyponomos*. This occurs as narrow, horizontal burrows up to 10 mm wide, but up to 700 mm in length (Trewin & McNamara 1995 figure 16), often in dense accumulations. The burrow infill structure sometimes shows a beaded structure.

HUNTING (PREDATION) TRACES

Heimdallia beds are often associated with the much larger horizontal burrow *Tumblagoodichnus* (Figures 23, 24). These are large burrows, generally 45–80 mm wide and horizontal to subhorizontal, and up to about 400 mm long, though most would be little more than half this

Figure 22   Bedding surface with feeding trace *Heimdallia* and microbial mats. Bottom of gorge western side of The Loop; FA2. Lens cap diameter 55 mm.

Figure 23 Bedding surface with extensive feeding trace *Heimdallia* and palimpsest ripples and the hunting burrow *Tumblagoodichnus*. Bottom of gorge western side of The Loop; FA2. Lens cap diameter 55 mm.

length. Where suitably preserved, the burrow shows a wide, convex median ridge. Trewin & McNamara (1995) suggested that the trace was made by an arthropod making 'scoops' into a wet sand surface, pushing the sand aside or upwards. Examples are known (Figure 24) where the sand has been pushed anteriorly and forms a crescentic mound at the front of the burrow, providing evidence for the direction of movement of the burrow creator. *Tumblagoodichnus* burrows in *Heimdallia*-rich beds could represent hunting traces made by the arthropod, feeding on the organism responsible for making the *Heimdallia* burrows.

Another trace fossil, *Didymaulichnus*, resembles *Tumblagoodichnus* in consisting of relatively short and narrow horizontal grooves with a central raised ridge (Trewin & McNamara figure 15). However, *Didymaulichnus* is an order of magnitude smaller than *Tumblagoodichnus*. It is less than 10 mm wide and rarely longer than about 50 mm. It inevitably occurs in clusters, so possibly represents grooves made by the same animal digging at a very shallow angle into the sediment.

Another association that further illustrates the well-developed trophic structures within this nascent freshwater ecosystem and which can possibly be interpreted as a predator–prey relationship, is the frequent co-occurrence of *Diplocraterion* with *Rusophycus* and *Selenichnites* (Figure 19). This latter ichnogenus is a crescentic hollow, deeper at one end than the other. Most are 40–60 mm in width, reaching maximum anterior depths of up to 20 mm. The anterior margin may be

inclined to vertical, or even overhanging in some instances (Trewin & McNamara 1995). The posterior end has a raised trefoil-shaped structure, which also occurs in *Rusophycus*. The lateral margins of *Selenichnites* may, like *Rusophycus*, sometimes show transverse scratch marks. *Selenichnites* can occur in very large numbers, with scores on the same bedding surface and often aligned in linear groups (Figure 25). These are likely to represent the activity of a single animal, repeatedly digging in the sand at low to high angles hunting for the *Diplocraterion* animal (Trewin & McNamara 1995 figure 33).

If *Rusophycus* represents the animal lying horizontally on a wet sand surface, then *Selenichnites* is the product of the arthropods' feeding behaviour. The occurrence of these dense clusters of *Selenichnites* and *Rusophycus* in sandsheet facies which are riddled with *Diplocraterion* suggest that the animal that made these U-shaped burrows was the target prey for the *Selenichnites*/ *Rusophycus* animal. As discussed above, the likelihood that *Rusophycus* was made by a euthycarcinoid, such as *Kalbarria*, implies that it was also responsible for *Selenichnites*.

Skolithos ichnofacies

LOCOMOTORY TRACES

These are rare in the *Skolithos* ichnofacies. A single well-developed *Diplichnites* trackway occurs south of Red Bluff, and is preserved in a thin-bedded, fine sandstone
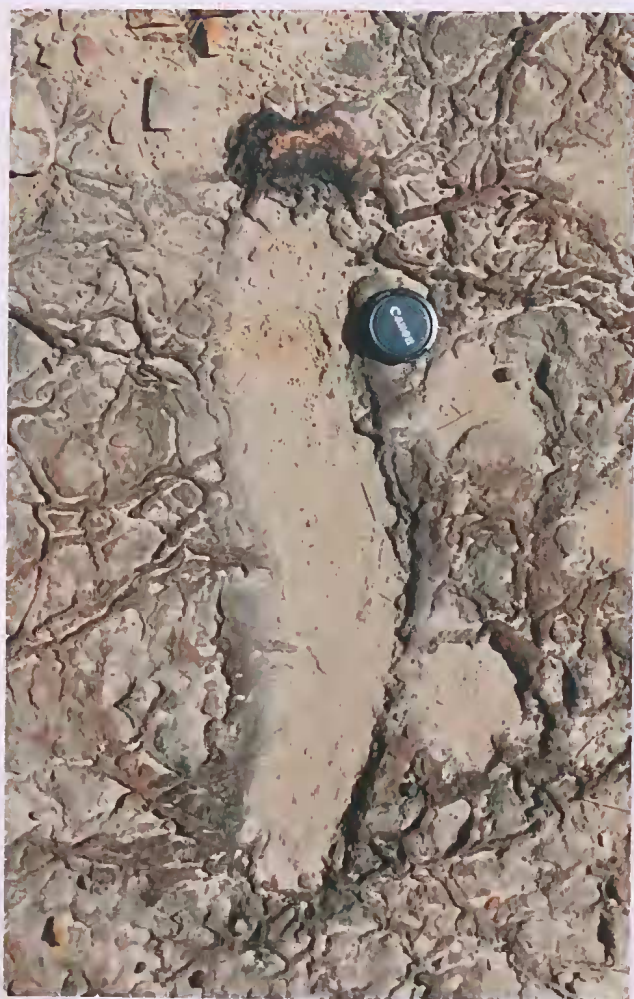
Figure 24 Hunting burrow *Tumblagoodichnus* in bioturbated bed of *Heimdallia* showing mound of sand pushed up by animal is it ploughed horizontally across the surface of the sand, presumably hunting for its prey; from surface in Figure 23. Lens cap diameter 55 mm.

reminiscent of the sand sheet facies of FA2. Even in the generally appreciably coarser sands of FA4 short segments of *Diplichnites* occur. The other locomotory trace *Aulichnites*, has not been found in the *Scoyenia* ichnofacies. It consist of sinuous, gently convex-upward trails, up to about 15 mm wide, with a weak longitudinal furrow (Figure 26). The traces can cover surfaces of many square metres. Although generally regarded as having been made by gastropods, Trewin & McNamara (1995) point out that arguments have been made for a xiphosurid origin (Chisholm 1985).

DWELLING TRACES

The most extensive dwelling traces are *Skolithos* (Figure 27). In the Tumblagooda Sandstone they consist essentially of vertical infilled burrows generally 10–15 mm in diameter, but sometimes up to 25 mm (Trewin & McNamara 1995). They may extend for up to 1 m in length and are particularly common in the upper part of FA4 in the area around Red Bluff (Figure 23). The burrows show slightly greater cementation than the surrounding sands, resulting in them weathering out from the surrounding sediment, perhaps due to the higher organic content in the burrows during early cementation. Although many of the numerous occurrences of *Skolithos* in other early Paleozoic clastic sequences are in sediments interpreted as being of shallow, high-energy marine origin, Woolfe (1990) suggested they may also be found in eolian, fluvial or even lacustrine settings (Netto 2007). Therefore, using *Skolithos* as an indicator of marine sedimentation may not always be appropriate.

The U-shaped burrow *Diplocraterion* in the *Skolithos* ichnofacies is generally larger than in the *Scoyenia* ichnofacies, with individual burrows up to 15 mm in diameter, paired openings spaced up to 50 mm apart and up to 100 mm deep. As Trewin & McNamara (1995) have observed, the forms of *Diplocraterion* in the Tumblagooda Sandstone are very similar to those that occur in the Early Devonian Old Red Sandstone in Scotland where

Figure 25 Hunting burrows *Selenichnites*, possibly made by just one or two individuals. Top of ridge, 500 km north of Nature's Window, The Loop; FA2. Pen is 12 cm long.

Figure 26 Locomotory trace *Aulichnites*. Car park 100 m north of Red Bluff; FA4.

Figure 27 Dwelling burrows *Skolithos*. Red Bluff. FA4.

they also occur with arthropod trackways in non-marine settings. Larger forms in the Tumblagooda Sandstone are closely associated with *Skolithos* burrows, such an association being typical of high-energy, mobile-sand settings.

Another dwelling burrow unique to FA4 is *Lunatubichnus* (Figure 28). These vertical burrows, up to 20 mm across and 70 mm deep have a crescentic cross-section, with a vertical groove often present in the convex inner wall. The crescentic cross-section is often, though not invariably, symmetrical. The burrows occur in clusters orientated in the same direction. Unlike *Skolithos*, these burrows are not infilled by sediment. The orientation of the burrows implies creation by a bilaterally symmetrical filter-feeding animal orientated into the direction of current flow (Trewin & McNamara 1995).

Figure 28 Dwelling trace *Lunatubichnus*. WAM 96.410a. Red Bluff. FA4. Scale bar 10 mm.

FEEDING TRACES

Evidence for possible feeding traces in the *Skolithos* ichnofacies is provided by the bell-shaped *Daedalus* (Trewin & McNamara 1995 figure 14). This trace consists of a vertical burrow shaft, the base of which flares out into a labyrinth of overlapping curving tubes, of similar width to the vertical shaft. The burrows are generally about 10 mm wide, with a vertical shaft up to 300 mm long and the basal bell-shaped convoluted burrows up to 120 mm across. Series of these burrows sometimes occur on single bedding planes, suggesting either a physical restriction to the depth of burrowing, or else attainment of an optimum feeding level. As Trewin & McNamara (1995) have pointed out, the similarity in form and size of the vertical shaft of *Daedalus* to *Skolithos* suggests the possibility that the two trace fossil types could have been constructed by the same type of animal.

Hocking (1991 figure 71) has illustrated a fine example of large burrows seen in cross-section, which might be attributable to either *Beaconites* or to *Tumblagoodichnus* in beds associated with *Skolithos*, suggestive of predatory activity by the larger horizontal burrow creator (R M Hocking pers. comm. 2013).

EARLY PALEOZOIC COLONISATION OF FRESHWATER AND TERRESTRIAL ENVIRONMENTS

The paleontological evidence for the colonisation of terrestrial and freshwater environments during the early Paleozoic comes not from body fossils but from studies of trace-fossil assemblages, such as those in the Tumblagooda Sandstone (Buatois & Mángano 1993, 2004, 2011; Buatois *et al.* 1998). By integrating trace fossil, sedimentological and paleobiological data dealing with the patterns of colonisation of the land by, predominantly, invertebrate biotas, the scope and extent of the first freshwater and terrestrial ecosystems can be established. Assemblages of trace fossils occur in a number of redbed early Paleozoic fluvial–lacustrine–eolian sequences that range in age from Late Ordovician to Devonian. This period represents a critical phase in the evolution of life on Earth. Not only were invertebrates and vertebrates beginning to migrate from aquatic environments onto the much harsher terrestrial world, but the evolution of terrestrial plants was

undergoing a profound revolution, as vascular plants evolved and expanded during this period.

Davies & Gibling (2010) have documented the profound effect that this botanical revolution had on river systems, and thus on sedimentological styles and preservation of evidence of the activity of the fledgling terrestrial biota. With the establishment of complex plant ecosystems during the Devonian, and their accompanying growth of extensive root systems, river systems changed from braided, laterally expansive outflows to constrained water flow in well-defined channels, with the trapping of finer, muddy fractions on alluvial floodplains. However, there is ample evidence to indicate that prior to the expansion of vascular plants, a range of invertebrates, and perhaps even vertebrates, had already begun to colonise the land and establish simple, but extensive, freshwater and subaerial ecosystems.

There are a number of contenders for pre-Silurian colonisation of the land by invertebrates, although whether these represent the establishment of nascent ecosystems, or just chance excursions onto land, is not clear. Kennedy & Droser (2011) suggested that as early as the beginning of the Cambrian, in the Wood Canyon Formation in California, millimetre-sized vertical burrows attributed to *Arenicolites* and *Skolithos*, along with the centimetre-scale horizontal burrow *Psammichnites*, were formed in fluvial channels. However, Davies & Gibling (2012) and McIlroy (2012) have argued against a non-marine depositional environment for these sediments, considering rather that the sediments were deposited in a marginal marine-influenced setting. More convincing evidence for subaerial trackways made by arthropods is found in Upper Cambrian to Lower Ordovician eolian dunes of the Nepean Formation in Ontario. These arthropods, attributed unconvincingly to euthycarcinoids, may have been making brief forays on to land, but not been part of any established terrestrial ecosystem.

Two Late Ordovician trace-fossil occurrences have been promoted as providing evidence of the activity of invertebrates in a non-marine environment. On the basis of trace fossils and paleosols, Retallack & Feakes (1987) and Retallack (2001) suggested that the Late Ordovician Juniata Formation in the eastern United States represents an early terrestrial ecosystem, with the dominant elements being burrowing millipedes that fed on non-vascular plants. Davies *et al.* (2010) have questioned this interpretation, arguing that there is insufficient evidence to ascribe the burrows to formation by millipedes, no evidence for plant material, and that the sediments could equally well be interpreted as having been deposited in a marginal marine environment. Trackways made by arthropods have been described from the Late Ordovician Borrowdale Volcanic Group in the English Lake District. These tracks, made on a wet, but subaerial, sand surface, are indicative, the authors consider, of periodic excursion by myriapod-like arthropods on to the land (Johnson *et al.* 1994).

None of these examples provide any convincing evidence for having been part of an established terrestrial or freshwater ecosystem. Such evidence would include not only a variety of subaerially formed trackways, whether made by invertebrates or vertebrates, but also indisputable living and feeding burrows preserved in sediments deposited either by fluvial or eolian agencies. Herringshaw & Solan (2008) have pointed out that recognising the first evidence for the colonisation of infaunality in shallow-marine environments, the colonisation of deep sea habitats and the colonisation of freshwater ecosystems in the terrestrial environments all come in the form of bioturbation. While our knowledge of the history of bioturbation in marine settings is well established, in the freshwater it is not. As Herringshaw & Solan (2008) have observed, the dwelling burrows that occur in the Tumblagooda Sandstone probably represent the earliest examples of such burrows. That, combined with a wide range of other dwelling burrows, hunting burrows, tracks and trails, point to the Tumblagooda Sandstone trace-fossil fauna as probably providing evidence of the oldest known establishment of relatively sophisticated trophic systems within a terrestrial freshwater ecosystem, in the early to mid-Silurian. This is contrary to the assertions of Buatois *et al.* (1998) and Buatois & Mángano (2011) that such ecosystems did not become established on land until the Silurian – Devonian boundary, penecontemporaneous with the evolution and rapid expansion of vascular plants. Assuming that Trewin's (1993a, b) freshwater hypothesis is correct, what the Tumblagooda Sandstone trace fossils indicate is that an arthropod-dominated terrestrial ecosystem predated the evolution of vascular plants, being present by the mid-Silurian.

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